Rice and Sturgeon Lakes Nutrient Budget Study

Trophic Interactions in Rice Lake III. Potential for Biomanipulation

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TROPHIC INTERACTIONS IN RICE LAKE III.

POTENTIAL FOR BIOMANIPULATION

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PREFACE

The Kawartha lakes are a large and economically important system of eight large lakes which are located in central Ontario. Sturgeon Lake and Rice Lake are located near the upper and lower ends of the Kawartha Lakes system respectively and both support significant amounts of urban and recreational development. They were chosen for detailed study because of their importance within the system and because both have shown the symptoms associated with excessive nutrient input for several years.

The Rice and Sturgeon Lakes Nutrient Budget Study was initiated to investigate linkages between point and non-point sources of nutrients, water quality, and aquatic life within the lakes and to estimate the impacts of these processes on in-lake water quality.

The study was supervised by the Rice - Sturgeon Lakes Nutrient Budget Technical Committee which had representatives from the Limnology Section (Water Resources Branch) and Central Region of the Ontario Ministry of the Environment and Energy, the Trent Severn Waterway (Environment Canada) and the Kawartha Lakes Fisheries Assessment Unit of the Ontario Ministry of Natural Resources.

This is one of a series of technical reports. These and the summary report (R/S Tech. Rep. No. 13) will provide a technical basis for the management of the Rice Lake and Sturgeon Lake ecosystems and for the use of land and water resources in the Kawartha Lakes region in general. A list of all reports in the R/S Tech. Rep. series is as follows:

1. Hutchinson N.J., B.J. Clark,, J.R. Munro and B.P. Neary 1993. Hydrological data for the watersheds of Rice Lake and Sturgeon Lake.1986 - 1989, 100 pp.

2. Hutchinson N.J., J.R. Munro, B.J. Clark and B.P. Neary. 1993. Water chemistry data for Rice Lake, Sturgeon Lake and their respective catchments. 1986-1989, 169 pp.

3. Hutchinson N.J., B.P. Neary, B.J. Clark and J.R. Munro 1993. Nutrient Budget data for the watersheds of Rice Lake and Sturgeon Lake. 120 pp.

4. Ryback, M. and I. Rybak. 1993. Sediment pigment stratigraphy as evidence of long term changes in primary productivity of Sturgeon and Rice Lakes (Kawartha Lakes). 24 pp.

5. Nicholls, K.H., M.F.P. Michalski and W. Gibson. 1993. Trophic interactions in Rice Lake I: An experimental demonstration of effects on water quality.

6. Limnos Ltd. 1993. Partitioning of phosphorus in *Potamogeton crispus*. 22 pp.

7. Limnos Ltd. 1993. Rice Lake macrophytes: distribution, composition, biomass, tissue nutrient content and ecological significance. 123 pp.

8. Beak Consultants Ltd. 1993. Release of phosphorus from Rice Lake sediments. 31 pp .

9. Limnos Ltd., Michael Michalski Associates and D.J. McQueen. 1993. Trophic interactions in Rice Lake II. Young-of-the-year yellow perch - *Daphnia* interactions, preliminary findings. 101 pp.

10. Badgery, J.E., D.J. McQueen, K.H. Nicholls and P.R.H. Schaap. 1993. Trophic interactions in Rice Lake III: Potential for biomanipulation. 1988 and 1989 .

11. Standke, S. 1993. The zooplankton of Rice Lake and Sturgeon Lakes, 1986-1988, Kawartha Lakes, Ontario .

12. Nicholls, K.H. 1993. The phytoplankton- water quality relationships of the Kawartha Lakes, 1972-1989.

13. Hutchinson, N.J., K.H. Nicholls and S.H. Maude, 1993. Rice and Sturgeon Lake Nutrient Budget Study: Summary and recommendations.

DISCLAIMER

This report was prepared for the Ontario Ministry of Environment and Energy as part of the Rice and Sturgeon Lakes Nutrient Budget Study. The views and ideas expressed in this report are those of the authors and do not necessarily reflect the views and policies of the Ontario Ministry of Environment and Energy. The mention of trade names and products does not constitute endorsement or recommendation of their use.

ABSTRACT

The potential for using biomanipulation to reduce algal standing stocks and improve water clarity was investigated during 1988 and 1989 at Rice Lake, Ontario, Canada. During both study years, fish bioenergetics simulations showed that for a short period in the spring, food consumption by young-of-the-year (YOY) yellow perch could account for almost all of the *Daphnia* (primarily *Daphnia galeata mendotae*) population losses that were calculated from a secondary production model applied to daphnids. However, during the summer, YOY perch densities decreased and the YOY perch community consumption rates became much lower than *Daphnia* production rates. This was associated with an order of magnitude increase in *Daphnia* biomass. Despite these dramatic summer increases in daphnid biomasses, chlorophyte and cyanophyte biovolumes and chlorophyll *a* concentrations increased more than five fold and Secchi depths decreased from spring values greater than 2 m to summer values less than 1 m. Through both summers, increased algal biomasses were associated with increased total phosphorus concentrations and with late spring die-backs of the extensive macrophyte beds (primarily *Potamogeton crispus*) that developed during the early spring. These data suggest that at Rice Lake, algal production and biomass is strongly influenced by bottom-up factors and it is unlikely that top-down biomanipulations of fish populations could stimulate additional *Daphnia* biomass or lead to the improvement of water clarity.

INTRODUCTION

Biomanipulation of piscivore stocks is frequently recommended as an in situ lake restoration technique (Hrbácek, 1962; Shapiro et al., 1975; Shapiro, 1980; Shapiro et al., 1982; Carpenter et al., 1985, 1987; Kitchell and Carpenter, 1988; Benndorf et al., 1988; Carpenter, 1989; Benndorf, 1990) intended to promote zooplankton grazing, decrease algal standing stocks and increase water clarity.

Rice Lake (surface area 100 km^2, mean depth 2.4 m) is a likely candidate for this treatment because it has a relatively uncomplicated pelagic food web structure (walleye, yellow perch, *Daphnia*, algae), and because phosphorus inputs are from non-point sources and are extremely difficult to control. The lake is located in an area of sedimentary deposits in south-central Ontario. It is eutrophic and long-term data sets (Anonymous, 1976) have established a consistent pattern of increasing summer total phosphorus concentrations accompanied by significant mid-summer blooms of blue-green algae. *Daphnia* spp (primarily *Daphnia galeata mendotae*) have been identified as the most significant crustacean herbivore in the lake, and YOY yellow perch (*Perca flavescens*) as their predominant predator (Nicholls et al., 1992 unpublished data). Predation on yellow perch is largely attributed to the walleye (*Stizostedion vitreum*) population in the lake.

We focused our fish assessments on YOY yellow perch because many studies have shown that they are obligate planktivores that can have significant negative impacts on *Daphnia* biomass (Mills and Forney, 1983; Post and McQueen, 1987; Vijverberg and van Densen, 1984). Also Nielsen (1980) found that consumption of

YOY yellow perch by walleye and adult yellow perch accounted for most of the deaths of YOY perch between June and October in Oneida Lake, New York. Because, Lake Oneida and Rice Lake have many similarities, our initial research hypothesis was that the Rice Lake YOY yellow perch might be holding the large zooplankton grazers (*Daphnia*) to such low levels that they were unable to control the algae. Our long-term plan was to use biomanipulation to solve this problem by stocking large numbers of walleye, an endemic species which has long been the most abundant piscivore in Rice Lake.

The purpose of the investigation reported here was to assess the potential efficacy of biomanipulation for Rice Lake. Our first objective was to determine whether YOY yellow perch could limit the development of the *Daphnia* community and our approach was to use bioenergetics simulations (Kitchell et al., 1974; Kitchell et al., 1977; Hewett and Johnson, 1987; Post, 1990) to estimate the impacts that young-of-the-year (YOY) yellow perch (Noble, 1968; Mills and Forney, 1983) might have on *Daphnia* biomass and production. Our second objective was to determine whether daphnids might be capable of influencing algal standing stocks and our approach was to investigate temporal empirical relationships between: (1) *Daphnia* (and total zooplankton) biomass, (2) phytoplankton biovolume and community composition, and (3) water chemistry.

METHODS

General Sampling Program

All samples were taken in the vicinity of Gores Landing near the western end of the lake at intervals ranging from 6 to 10 days. Sampling began in May in both years and continued until August in 1988 and September in 1989. We sampled three stations: (1) an inshore station, (100 m from the shoreline at a depth of 2.2 m) where macrophytes were abundant for more than 80% of the sampling period, (2) a mid-depth station (3.5 m deep and 500 m from shore) where macrophytes were also abundant through most of the sampling season and (3) an offshore station (5 m deep), where macrophytes were never visible from the surface. In the results that follow, the "littoral" samples represent (the mean of stations 1 and 2) and the "open-water" samples represent (station 3).

Physical-chemical conditions

In 1988, temperatures were measured using continuous-recording thermometers (Ryan Instruments) and in 1989, temperature profiles at each station were measured with a YSI model 54 meter on each sampling date. Mid-water estimates were used for the bioenergetics simulations. In both years, water clarity was measured on each sampling date using a standard 20 cm black-and-white Secchi disk. Water samples were collected at the open water station and chlorophyll *a* and total phosphorus were determined by the Ontario Ministry of the Environment (Anonymous, 1981).

Phytoplankton

Phytoplankton samples (0 - 4 m integrated samples) from the open water station were analyzed at the Ontario Ministry of the Environment. Individual cells were counted, measured and identified to genus using an inverted microscope, and then both abundance and biovolume were calculated for all taxa (Nicholls and Carney, 1979).

Zooplankton

Weekly zooplankton samples were collected at 1 m depth intervals from each station using a 35 L plexiglass trap (Schindler, 1969) with a 80 µm mesh net. On each sampling date two sets of zooplankton samples were collected. One set was collected for zooplankton identification, abundance and biomass determination. These were preserved with 4% formalin solution (Prepas, 1978). The other set was collected for lipid-ovary and egg counts. They were stored in soda water, set on ice, and then frozen upon return to the laboratory.

The lipid index developed by Goulden and Hornig (1980) and later modified to a lipid-ovary index (L-O) (Tessier and Goulden, 1982) was used to rank-score the amount of lipid stored in the hemocoele and to rank the size and opaqueness of ovaries. The samples collected for this analysis were thawed at room temperature and counted immediately to prevent deterioration after thawing. The number of females with eggs and the egg numbers were also recorded. A modified *Daphnia* L-O statistic was calculated by plotting the L-O index (Tessier and Goulden, 1982) with

respect to body length for each sampling date and then taking the slope of the best-fit line as described by y=bx. We used the slope of the regression line as a modified L-O statistic which was correlated with the physiological condition of the *Daphnia* (by the amount of stored lipid) and free of bias caused by animal size.

Zooplankton biomasses were estimated using a computer assisted calliper device (Sprules et al., 1981). Zooplankton were identified to family for cladocerans (chydorids, *Daphnia*, other daphnids, bosminids and sidids) and to suborder or developmental stage for copepods (cyclopoids, calanoids, and nauplii). On average, 200-300 animals were counted and measured for each sample.

YOY yellow perch and other fish species

In 1988, fish samples were taken at weekly intervals between May 12 and July 12. Two collection methods were used to monitor the YOY yellow perch abundance in the lake. A Miller trawl with a 500 µm mesh, set at a depth of 0.75 m (Noble, 1968) was used for the initial 3 collections. On average, six samples were collected at three sampling locations. A cross calibration between the Miller trawl and a 46 m x 6 m fine mesh (1 mm mesh purse seine) was carried out on the third fish sampling date (May 30, 1988) (Table 1). At that time, the purse seine was found to be more efficient at catching the YOY perch and we switched to the purse seine for subsequent collections. During 1989, fish samples were collected weekly, between June 6 and July 12. Only the purse seine was used and samples were taken from all three stations as in 1988. During each collection period, a subsample of unpreserved YOY

yellow perch was stored in soda water, placed on ice and returned to the laboratory for analysis of length, weight and stomach contents. The remaining YOY yellow perch and all other fish species caught were also preserved in 20% formalin.

YOY yellow perch from the fish collections were identified (Auer, 1980) and enumerated. Lengths and weights of 50 YOY perch individuals were measured for each date for growth analysis. Stomach content analysis was based on 10 perch from each of the sample dates. Prey found in the fish stomachs were identified and counted using the methods described for the zooplankton analysis.

***Daphnia* production**

Daphnia (primarily *D. g. mendotae*) production was calculated for the periods between successive sampling dates. Calculations were made for the open-water site in 1988 and for both sites in 1989. The formulas used are from Cooley et al. (1986):

$$P = (N_2 - N_1)\ (b/r)\ w$$

$$b = \ln\ ((((N_{eggs1}\ L^{-1})/N_1) + ((N_{eggs2}\ L^{-1})/N_2))/2 + 1)/K$$

$$r = (\ln N_2 - \ln N_1)/t$$

where P is production ($\mu g\ L^{-1}\ d^{-1}$), N_2 = numbers of *Daphnia* L^{-1} at sampling time i+1, N_1 = numbers of *Daphnia* L^{-1} at sampling time i, b = instantaneous birth rate, K = egg development time (Hall, 1964), r = instantaneous population growth rate, and w = mean individual *Daphnia* biomass (μg) between successive sampling dates. We

determined loss rates by subtracting observed weekly increments from the calculated weekly production.

Consumption by YOY Yellow Perch

A general bioenergetics model of fish growth (Hewett and Johnson, 1987) was used with the physiological parameters appropriate for YOY yellow perch (Post, 1990). The caloric density of the perch and their prey was assumed to be equivalent (Post, 1988). The Rice Lake data set (temperature, growth, diet, density and mortality) was used with the model to calculate weight specific YOY yellow perch consumption rates. For the 1988 data, population survivorship was modelled as a negative exponential line of best fit through the population density data. For the 1989 data, the original field data were used. For both years, the model was used to calculate total YOY consumption per cubic metre per day of *Daphnia* and other zooplankton by YOY yellow perch. These were compared with *Daphnia* community losses calculated from the secondary production model and the field data.

RESULTS

Chemical conditions and standing stocks

The mid-water column temperatures were generally higher in 1988 than in 1989 (Table 2). Total phosphorus concentrations generally increased during both years (Table 2). Secchi depths at all stations decreased through the spring and summer in both years (Fig. 1) and chlorophyll *a* (Fig. 2) and algal biovolumes (Fig. 3) increased during July and remained high throughout the summer and fall. Of the blue-green algae, the most common genera were *Anabaena* and *Microcystis* while the predominant diatom genus was *Melosira* (Table 3). The common Chlorophyceae genera were *Chlorella* and *Oocystis* (Table 3).

During both years, at both stations, *Daphnia* (Fig. 4) comprised the major portion of the total zooplankton biomass (Fig. 5). *Daphnia* fluctuated during the spring, increased in July and gradually decreased through the rest of the summer. The biomass values in 1989 tended to be lower than in 1988, particularly during the first few months of the study period. In both years, the number of *Daphnia* eggs L^{-1} remained low until the end of June (Table 4) and increased through July. During both years, the modified lipid-ovary statistic was highest in July and August (Table 4). In both 1988 and 1989, estimates of *Daphnia* production were low during the spring and increased rapidly through the first two weeks of July.

In 1988, the YOY perch density (Table 5) was highest in the open-water habitat in early spring. By the second week of June, densities in the two habitats were similar and during the rest of the sampling period, fish were found only in the littoral area.

The pattern of YOY perch density (Table 6) in 1989 was similar to 1988 with higher numbers in the open-water in early June and higher numbers in the littoral habitat for the remainder of the period.

During both years, YOY yellow perch stomach content analysis showed that as the size of the perch increased, there was a corresponding increase in preference for *Daphnia* (Table 7). *Bosmina* and cyclopoids were also important in both years and *Ceriodaphnia* were important during 1989.

YOY yellow perch were by far the most abundant fish species caught in both years. Other fish species in order of decreasing abundance, included: YOY pumpkinseeds, adult bluegills, adult yellow perch, adult pumpkinseeds, adult spot-tailed shiners, adult golden shiners and adult walleye.

Fish - Daphnia interactions

During both years, the greatest losses to the *Daphnia* community occurred during the month of July. There were also losses to the populations at the end of May in 1988, and during August 1989 (Table 4). In contrast, *Daphnia* consumption by YOY yellow perch was relatively constant through June and July of both years (Fig. 6).

In 1988, *Daphnia* consumption by yellow perch made up 43% of the total *Daphnia* loss during the interval from May 19 to 30, and over 100% between May 30 and June 14 (Table 4 and Fig. 6). Later in the summer, consumption by the YOY perch accounted for almost none of the total *Daphnia* loss. During 1989, there were fewer time periods when the YOY perch population in the lake could have

accounted for the *Daphnia* population losses.

Zooplankton, phytoplankton and water clarity

Daphnia biomass (Fig. 4) tended to be lower during the spring than in July and August while Secchi depth (Fig. 1) was highest in May and June and decreased throughout the summer. These opposing trends in Secchi depth and *Daphnia* biomass were even more obvious in 1989 than in 1988 and correlations (Fig. 7) of Secchi depth and *Daphnia* biomass revealed weak negative relationships which were not significant ($p > 0.05$)

The relationship between *Daphnia* biomass and chlorophyll *a* concentration (Fig. 8) also revealed no significant relationships ($p > 0.05$) for either 1988 or 1989. Time lag analyses showed that high *Daphnia* biomass in one week did not lead to low chlorophyll *a* concentrations the next week.

Phytoplankton and Phosphorus

During both years there were significant positive correlations between total phosphorus and chlorophyll *a* ($p < 0.001$) (Fig. 9).

DISCUSSION

Our results have caused us to reconsider our plan to biomanipulate fish stocks in Rice Lake. It is clear that during both years, YOY yellow perch had significant negative impacts on *Daphnia* biomass only during the spring before YOY numbers decreased and that during the summer months, *Daphnia* were able to increase dramatically in both onshore and offshore habitats. Also during the summer months, *Daphnia* production was always considerably higher than YOY yellow perch consumption.

It is widely accepted that predation plays an important role in determining zooplankton community structure, however, food limitation and temperature effects are also important (Lampert and Schober, 1980; Benndorf and Horn, 1985; Gliwicz, 1985; Threlkeld, 1985; Vanni, 1987). During both years, *Daphnia* production and egg numbers were lowest during May and highest during July. Hall (1964) found that temperature was the primary factor influencing duration of egg development, frequency of reproduction and life span in *Daphnia*. This is consistent with the observation that during 1989, spring temperatures were lower and *Daphnia* production rates were also lower than during 1988. The losses to the *Daphnia* population during 1989 were also smaller than in 1988. This was almost certainly due in part, to lower numbers of YOY yellow perch, but might also be attributed to decreased intraspecific competition (Vanni, 1987). During 1989, the algal density was much higher than during 1988 and *Daphnia* L-O statistics were consistently higher.

Contrary to the predictions of cascading trophic interaction and biomanipulation theories, the Rice Lake data set did not yield significant correlations between *Daphnia* biomass and chlorophyll concentrations or water transparency. Several studies (summarized in McQueen et al., 1986, 1989 and McQueen, 1990), describe similar patterns. They suggest that for eutrophic lakes, clear-water phases often occur during the spring and are often correlated with high *Daphnia* biomass (Lampert et al., 1986), but during the summer these periods of clear-water are replaced by high chlorophyte biomasses and reduced grazing efficiency by *Daphnia* and other zooplankton.

There are many studies which have investigated the relationship between total phosphorus concentration and algal standing crop (Dillon and Rigler, 1974; Schindler, 1978; Prepas and Trew, 1983) and all have found highly significant correlations between these two variables. The significant positive correlations found between total phosphorus and chlorophyll *a* concentrations in this study corroborate these findings. These correlations suggest that at Rice Lake, low spring algal concentrations were associated with low total phosphorus concentrations and the higher summer algal biomasses were associated with the increased total phosphorus concentrations that resulted from macrophyte die-off, wind induced internal loading and external loading from seasonal use of cottages and farmlands.

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Table 1. Calibration of the Miller trawl vs the purse seine conducted in 1988.

Date	Station	Time of day	Catch average (m^{-3})	
			Purse seine	Miller trawl
1988				
May 30	Openwater	Day	0.942	0.217 (23% of seine catch)
May 30	Openwater	Dusk	0.828	0.611 (74% of seine catch)

Table 2. Total phosphorus ($\mu g\ L^{-1}$) and temperatures (degrees C) during 1988 and 1989 at the inshore and offshore stations.

Date		Phosphorus		Temperature	
		Inshore	Offshore	Inshore	Offshore
1988					
May	12	---	21.0	---	14.6
	19	---	23.0	---	14.3
	30	---	22.0	---	18.3
June	7	---	26.0	---	18.7
	14	---	21.0	---	19.5
	21	---	24.0	---	21.5
	28	---	36.0	---	19.6
July	5	---	24.0	---	18.6
	12	---	19.0	---	22.9
	19	---	28.0	---	26.0
	29	---	40.0	---	24.5
Aug	8	---	---	---	24.5
	15	---	36.0	---	---
1989					
May	4	23.5	28.0	8.4	8.0
	9	20.0	19.0	8.6	8.3
	16	22.0	19.0	12.7	11.8
	23	22.0	21.0	16.4	16.5
	31	23.5	15.0	16.6	15.9
June	6	---	---	17.9	17.9
	13	26.0	21.0	17.8	17.7
	21	32.0	23.0	18.0	17.9
	28	35.0	31.0	22.5	21.8
July	7	---	---	25.5	24.9
	12	27.0	28.0	23.5	22.9
	18	38.0	49.0	21.6	21.3
	25	56.5	42.0	24.9	23.4
Aug	2	55.0	45.0	22.0	22.2
	8	56.5	63.0	20.0	19.9
	16	56.5	47.0	20.7	20.8
	22	94.5	57.0	20.1	20.1
Sept	21	72.5	67.0	15.4	15.4

Table 3. Dominant phytoplankton genera in 1989 which constituted more than 15% of the total phytoplankton abundance.

	DIATOMS	GREENS	BLUE-GREENS
May	*Synedra*	*Chlorella*, *Oocystis*	
June	*Melosira*	*Chlorella*	
July	*Melosira*		*Anabaena*, *Microcystis*
August	*Melosira*		*Anabaena*, *Microcystis*
September		*Ankistrodesmus*	*Anabaena*

Table 4a. Calulations of Daphnia secondary production ($\mu g\ L^{-1}\ d^{-1}$), observed daily losses or gains ($\mu g\ L^{-1}\ d^{-1}$), and calculated daily losses or gains ($\mu g\ L^{-1}\ d^{-1}$) for the 1988 offshore station.

Date	No. L^{-1}	Biomass ($\mu g\ L^{-1}$)	Mean individual biomass	Eggs L^{-1}	LO Statistic	Production	Observed gains or losses	Calculated gains or losses
May 12	0	0	---	---	---			
						0	+ 155	+ 155
19	19	1085	57.1	4.6	0.6			
						35	- 70	- 105
30	5	318	66.4	0	0.8			
						4	- 18	- 22
June 7	6	173	28.4	0.7	0.7			
						4	- 23	- 27
14	1	14	36.5	0	0.2			
						0	+ 172	+ 172
21	16	1222	76.4	0	0.6			
						284	+ 683	+ 399
28	57	6001	105.1	51.4	0.8			
						1794	+1399	- 395
July 5	197	15793	80.3	196.6	1.1			
						3181	-1685	-4866
12	58	4001	68.6	0	0.8			
						471	+ 186	- 285
19	76	5301	70.0	31.8	0.9			
						732	- 46	- 778
29	50	4838	95.8	0	1.2			
						606	- 361	- 967
Aug 8	19	1219	64.2	10.3	0.9			

Table 4b. Calulations of Daphnia secondary production ($\mu g\ L^{-1}\ d^{-1}$), observed daily losses or gains ($\mu g\ L^{-1}\ d^{-1}$), and calculated daily losses or gains ($\mu g\ L^{-1}\ d^{-1}$) for the littoral site in 1989.

Date	No. L^{-1}	Biomass ($\mu g\ L^{-1}$)	Mean individual biomass	Eggs L^{-1}	LO Statistic	Production	Observed gains or losses	Calculated gains or losses
May 4	0	0	---	---	---			
						0	0	0
9	0	0	---	---	---			
						0	+ 8	+ 8
16	3	52	18.3	0	---			
						1	- 8	- 9
23	0	0	---	---	---			
						0	+ 1	+ 1
31	0	---	---	---	---			
						0	- 1	- 1
Jun 6	0	0	---	---	---			
						0	+ 14	+ 14
13	1	97	107.8	0.9	1.1			
						2	+ 17	+ 15
21	6	230	41.1	0.3	1.3			
						24	+170	+146
28	25	1422	59.3	8.9	1.2			
						99	+ 8	- 91
Jul 7	56	1499	27.1	0	1.2			
						204	+113	- 91
12	60	2065	34.4	28.8	1.9			
						275	+810	+535
18	164	6924	42.2	0	0.8			
						91	-560	-651
25	95	3002	31.8	5.7	1.2			
						425	-264	-689
Aug 2	9	892	95.9	2.1	1.3			
						88	- 35	-123
8	11	682	63.8	3.2	1.4			
						114	+ 35	- 79
16	16	965	60.7	8.3	1.9			
						118	- 69	-187
22	19	554	28.6	5.5	1.3			
						65	+ 30	- 35
Sep 17	20	1329	66.5	2.8	0.8			

Table 43. Calculations of *Daphnia* secondary production ($\mu g\ L^{-1}\ d^{-1}$), observed daily losses or gains ($\mu g\ L^{-1}\ d^{-1}$), and calculated daily losses or gains ($\mu g\ L^{-1}\ d^{-1}$) for the open-water site in 1989.

Date	No. L^{-1}	Biomass ($\mu g\ L^{-1}$)	Mean individual biomass	Eggs L^{-1}	LO Statistic	Production	Observed gains or losses	Calculated gains or losses
May 4	0	0	---	---	---			
						0	+ 1	+ 1
9	1	6	6	0	---			
						1	+ 2	+ 1
16	1	20	20	1.3	---			
						1	- 2	- 3
23	0	0	---	---	---			
						0	+ 11	+ 11
31	2	89	44.5	0.3	1.3			
						6	+ 32	+ 26
Jun 6	10	282	28.2	3.8	1.9			
						27	- 39	- 66
13	1	5	5	0.4	1.5			
						2	+ 107	+ 105
21	13	868	66.7	1.1	1.3			
						57	- 60	- 117
28	5	446	89.2	1.0	1.8			
						142	+ 557	+ 416
Jul 7	44	5460	124.1	37.6	1.8			
						2283	- 4	-2287
12	68	5436	79.9	10.9	1.9			
						292	+ 566	+ 274
18	138	8834	64.5	11.0	1.5			
						392	-1012	-1404
25	35	1746	49.9	4.3	0.9			
						142	- 9	- 151
Aug 2	23	1667	75.8	3.1	1.7			
						222	- 182	- 404
8	15	572	38.1	9.8	1.4			
						311	+ 152	- 159
16	28	1793	64.1	35.6	2.2			
						715	+ 81	- 634
22	31	2284	73.7	16.3	1.7			
						253	+ 8	- 245
Sep 17	40	2508	62.7	8.0	1.4			

Table 5. 1988 yellow perch YOY population estimates (mean number m^{-3}) and mean individual fish weights (grams). Miller trawls were used for the first 3 dates and purse seines for the next 6 dates. Numbers of net sets and trawls are shown in parentheses. Mean individual weights are based on 50 measurements per time period.

Sample date	Mean population estimate (numbers $m^{-3} \pm 1$ SD)	Mean individual weight (g)
1988		
May 12	19.95 ± 18.5 (14)	0.0014
19	1.76 ± 2.14 (15)	0.0047
30	0.58 ± 0.68 (15)	0.0237
June 7	4.04 ± 6.41 (15)	0.0766
14	1.79 ± 1.85 (14)	0.1514
21	0.26 ± 0.51 (11)	0.2502
28	0.08 ± 0.11 (14)	0.4693
July 5	0.02 ± 0.05 (15)	0.7069
12	0.03 ± 0.04 (13)	1.044

Table 6. 1989 yellow perch YOY population estimates (mean number m^{-3}) and mean individual fish weights (grams). Purse seines were used on all dates. Numbers of net sets and numbers of fish measured are shown in parentheses.

Sample date	Mean population estimate (numbers m^{-3} ± 1 SD)	Mean individual weight (g ± 1 SD)
1989		
June 7	2.63 ± 2.31 (9)	0.060 ± 0.017 (25)
14	0.80 ± 0.54 (9)	0.155 ± 0.031 (40)
21	0.14 ± 0.18 (6)	0.310 ± 0.066 (25)
28	0.31 ± 0.38 (9)	0.550 ± 0.118 (39)
July 7	0.005 ± 0.004 (9)	1.317 ± 0.420 (7)
12	0.013 ± 0.014 (6)	———

Table 7. YOY yellow perch stomach contents collected during 1988 and 1989. Proportion representation is based on biomass estimates. Cyclopoida = Cyc., bosminid = Bos., *Daphnia* = Dap., chydorid = Chy., ceriodaphnid = Ceri., *Leptodora* = Lep., *Diaphanosoma* = Diap., insect larvae = Ins.

Date	Percent representation							
	Cyc.	Bos.	Dap.	Chy.	Ceri.	Lep.	Diap.	Ins.
1988								
May 30	60	25	15	0	0	0	0	0
Jun 7	5	50	20	25	0	0	0	0
14	5	35	30	30	0	0	0	0
21	10	5	70	5	5	0	0	5
28	0	0	95	0	2	0	0	2
Jul 12	3	2	80	0	10	2	0	3
1989								
Jun 6	76	13	6	0	2	0	3	0
13	36	54	6	2	0	0	2	0
21	3	66	1	2	24	0	3	1
28	9	9	3	1	71	0	6	1
Jul 7	38	0	37	0	0	3	0	20

Appendix 1. Bioenergetics model data input and results output for 1988 and 1989.

Date	Julian days	Water Temperature	Individual fish weight (g)	Fish density (numbers m^{-3})	Fish biomass (g m^{-3})	Wet weight *Daphnia* eaten d^{-1} ($\mu g\ L^{-1}$)	Wet weight *Daphnia* production ($\mu g\ L^{-1}$)
1988							
May 12	132	14.6	0.0014	36.2	0.051		
						26.3	0.1
19	139	14.3	0.0047	18.1	0.085		
						38.9	35.0
30	150	18.3	0.0237	6.2	0.146		
						38.1	4.0
June 7	158	18.7	0.0766	2.8	0.215		
						31.6	4.0
14	165	19.6	0.1514	1.4	0.214		
						56.1	0.1
21	172	21.5	0.2502	0.7	0.177		
						66.9	284.0
28	179	19.7	0.4693	0.2	0.167		
						39.8	1794.0
July 5	186	18.6	0.7069	0.13	0.127		
						32.1	3181.0
12	192	22.9	1.0440	0.1	0.007		

Appendix 1 continued

1989								
June	7	157	17.9	0.073	3.13	0.230		
							9.8	27.0
	14	164	17.7	0.156	0.64	0.099		
							4.1	2.0
	21	171	17.9	0.285	0.15	0.044		
							0.8	57.0
	28	178	21.8	0.582	0.03	0.015		
							2.8	142.0
July	7	187	24.9	0.98	0.03	0.032		
							3.9	2283.0
	12	193	22.9	1.30	0	0		

LIST OF FIGURES

Figure 1. Secchi depth (meters) with respect to time for 1988 (open symbols) and 1989 (solid symbols). Open-water stations = △ (1988) and ▲ (1989) and littoral station = ● (1989).

Figure 2. Chlorophyll *a* concentrations (ug L^{-1} d^{-1}) with respect to time for 1988 and 1989. Open-water stations = △ (1988) and ▲ (1989) and littoral station = ● (1989).

Figure 3. Phytoplankton biovolumes (um^3) for the open-water station for 1988 (open symbols) and 1989 (solid symbols). The total biovolumes = ■, □ and cyanophyte biovolumes = ●, ○.

Figure 4. *Daphnia* biomass (ug L^{-1} d^{-1} fresh weight) with respect to time for 1988 and 1989. Open-water stations = △ (1988) and ▲ (1989) and littoral stations = ○ (1988) and ● (1989).

Figure 5. Zooplankton biomass (ug L^{-1} d^{-1} fresh weight) with respect to time for 1988 and 1989. Open-water stations = △ (1988) and ▲ (1989) and littoral stations = ◯ (1988) and ● (1989).

Figure 6. *Daphnia* production (ug L^{-1} d^{-1} fresh weight) and consumption (ug L^{-1} d^{-1} fresh weight) by YOY yellow perch with respect to time for 1988 and 1989.

Figure 7. Mid-water station Secchi depth (meters) with respect to *Daphnia* biomass (ug L^{-1} d^{-1} fresh weight) for 1988 (◯) and 1989 (●).

Figure 8. Mid-water chlorophyll *a* concentrations (ug L^{-1} d^{-1}) with respect to *Daphnia* biomass (ug L^{-1} d^{-1} fresh weight) for 1988 (◯) and 1989 (●).

Figure 9. Mid-water chlorophyll *a* concentrations (ug L^{-1} d^{-1}) with respect to phosphorus concentrations (ug L^{-1} d^{-1}) for 1988 (◯) and 1989 (●).

FIGURE 1

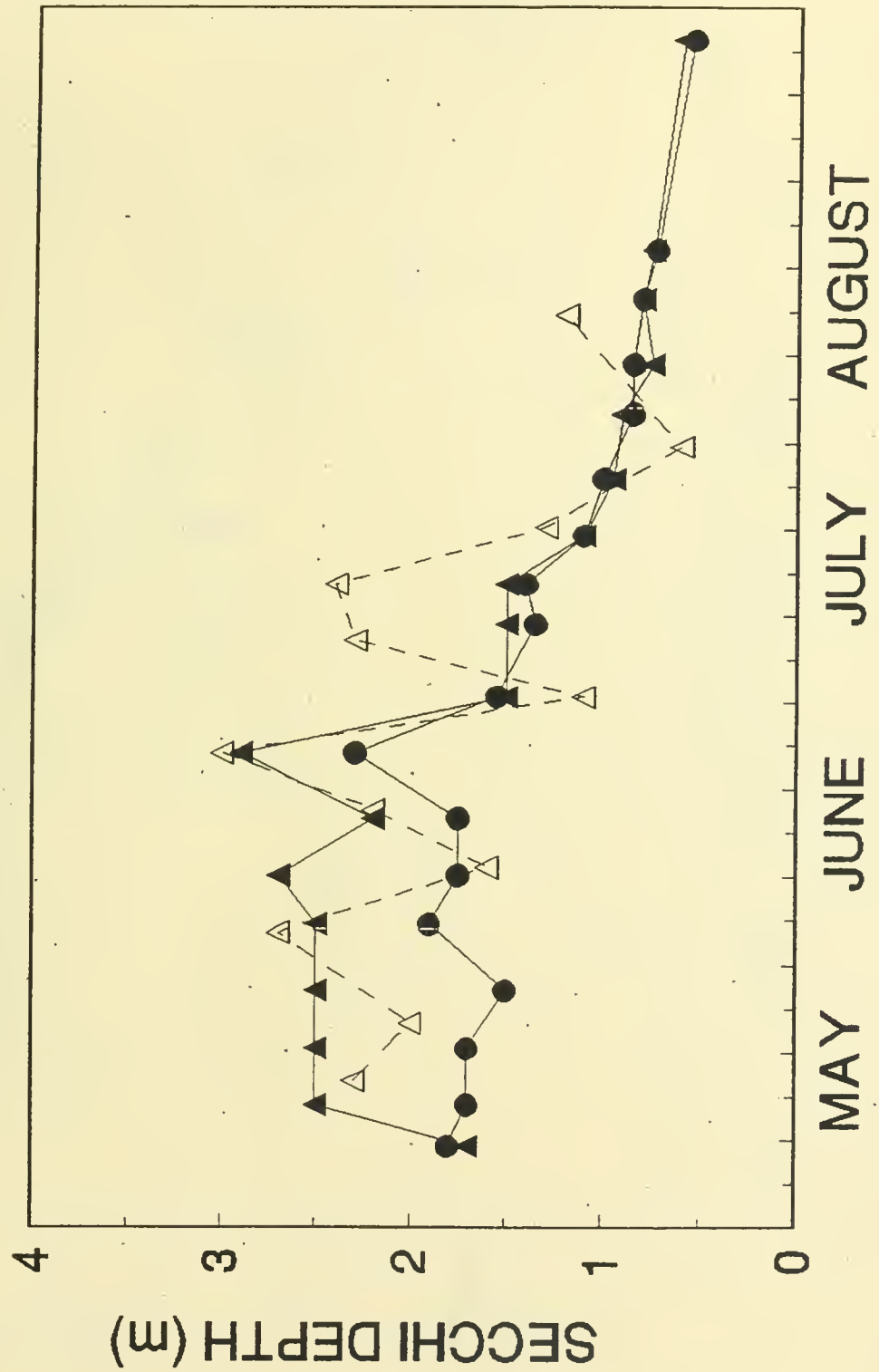

FIGURE 2

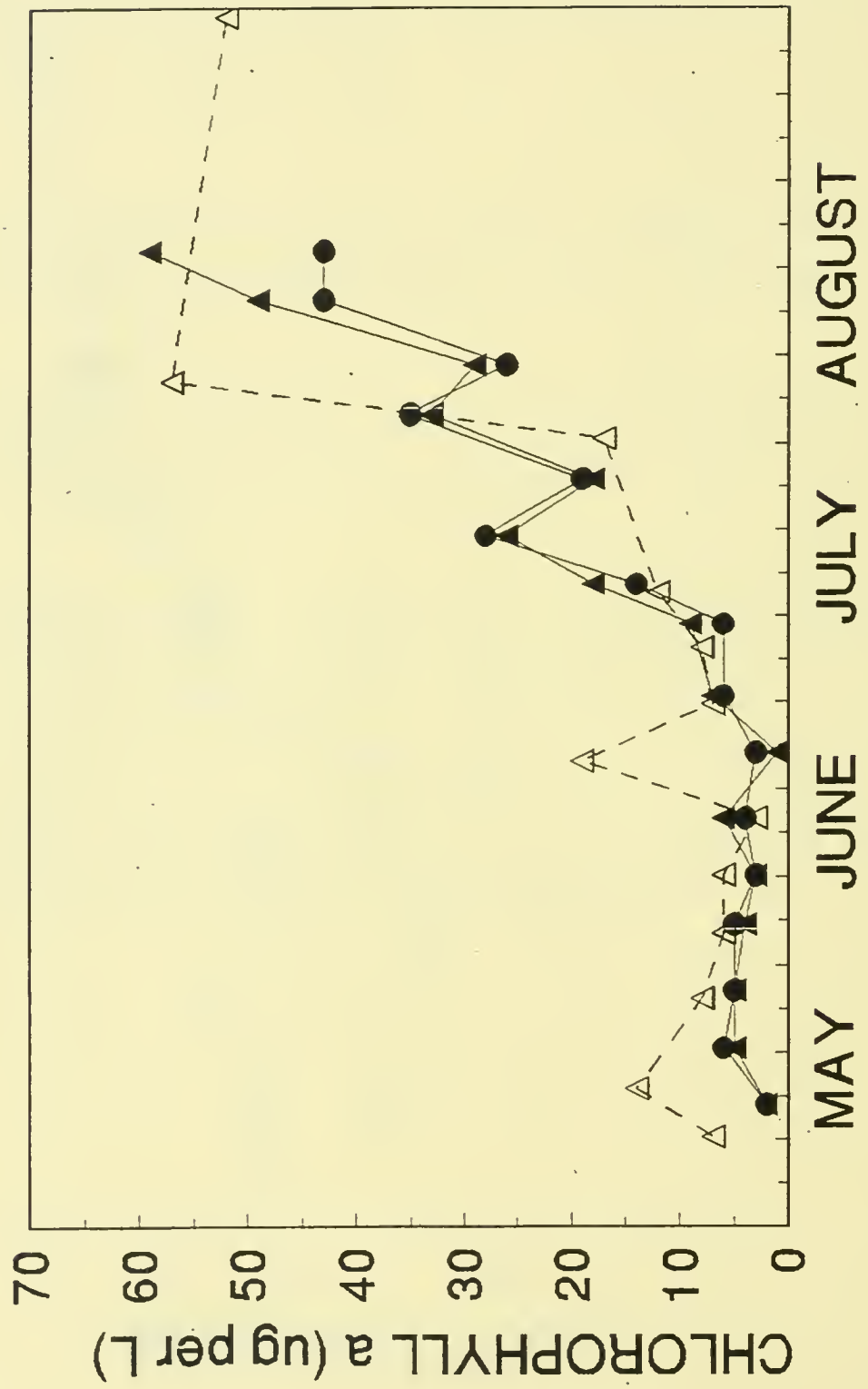
CHLOROPHYLL a (ug per L)
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST

FIGURE 3

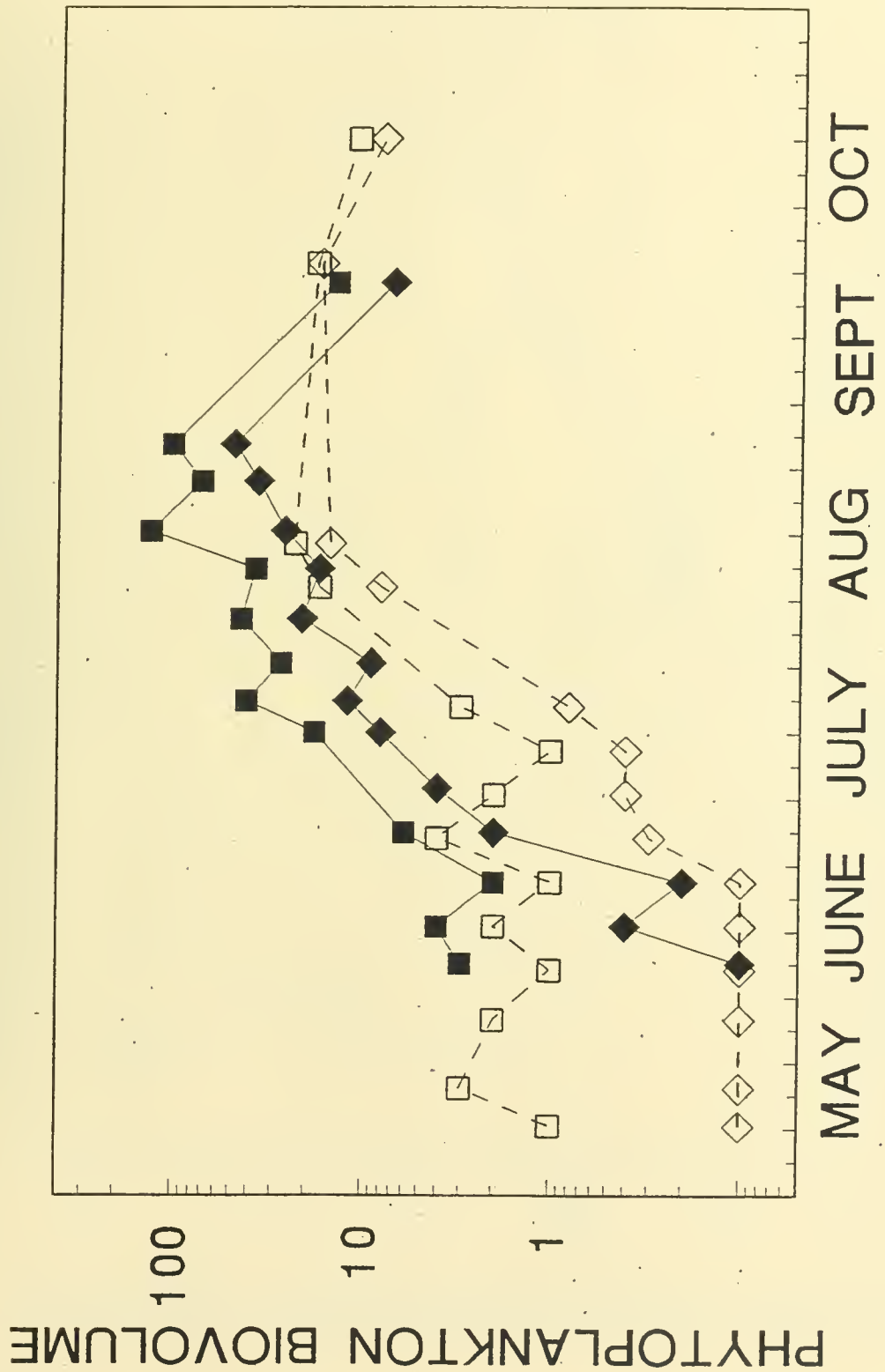

FIGURE 4

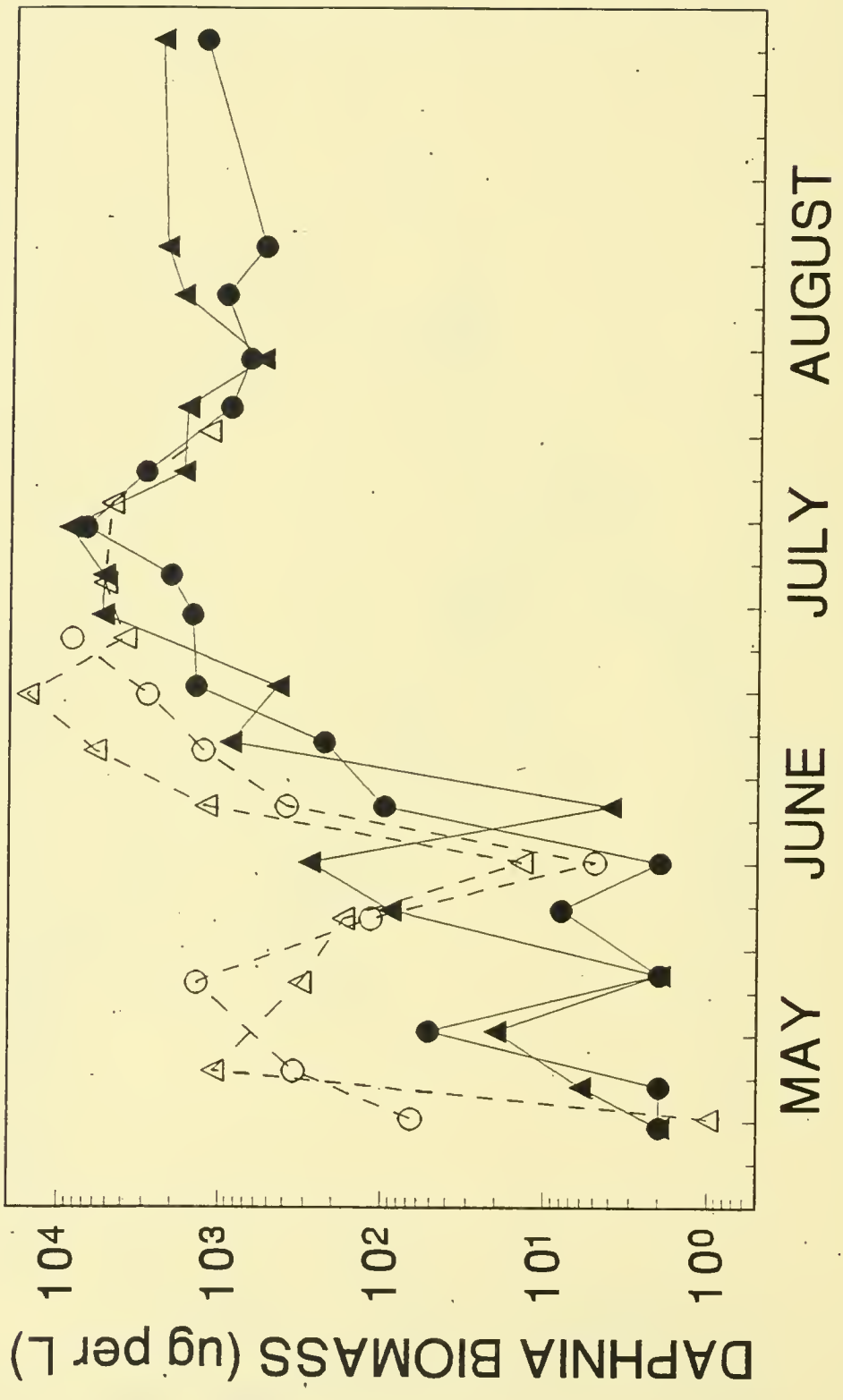
DAPHNIA BIOMASS (ug per L)
10⁴
10³
10²
10¹
10⁰
MAY
JUNE
JULY
AUGUST

FIGURE 5

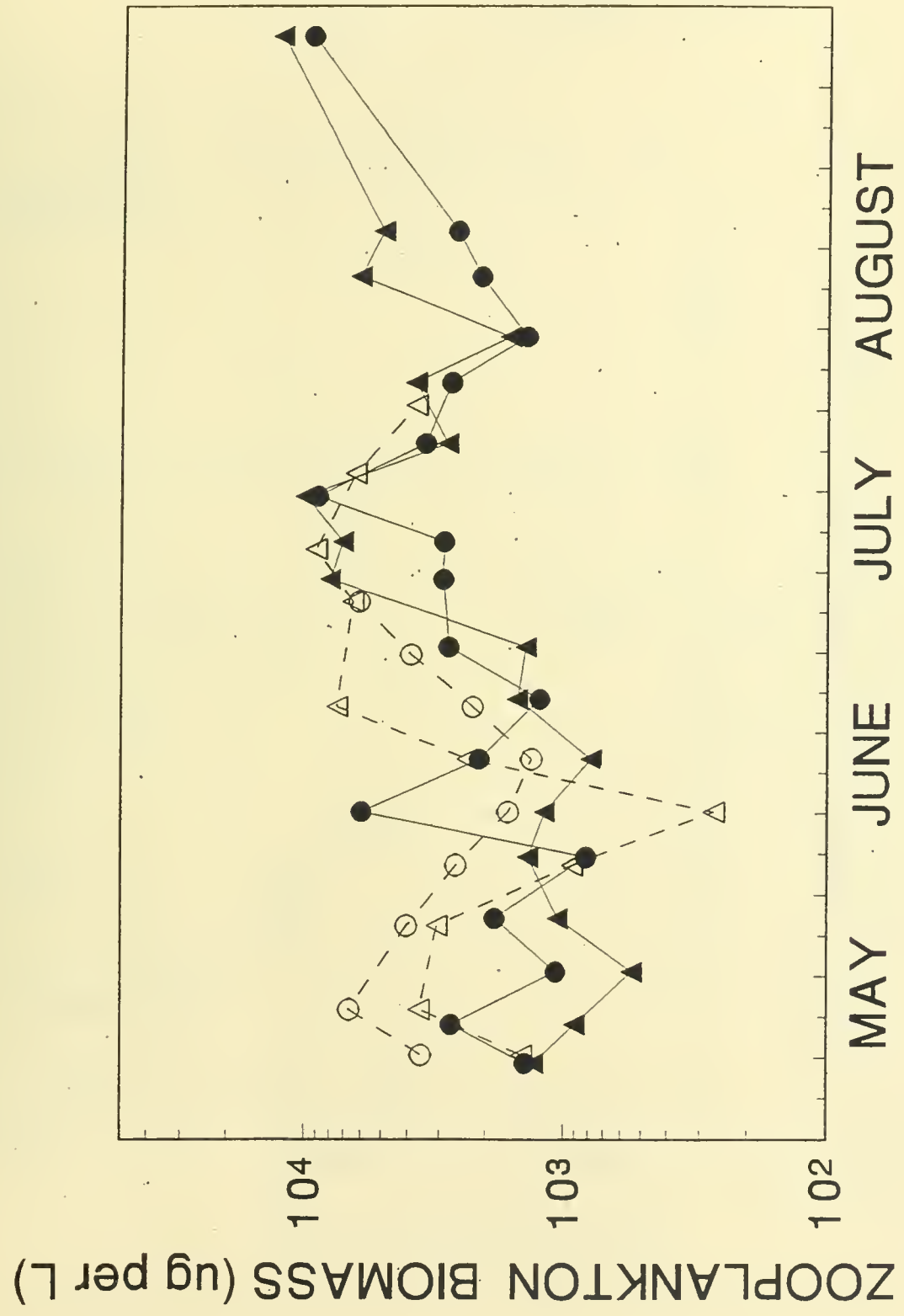
ZOOPLANKTON BIOMASS (ug per L)
10⁴
10³
10²
MAY
JUNE
JULY
AUGUST

FIGURE 6

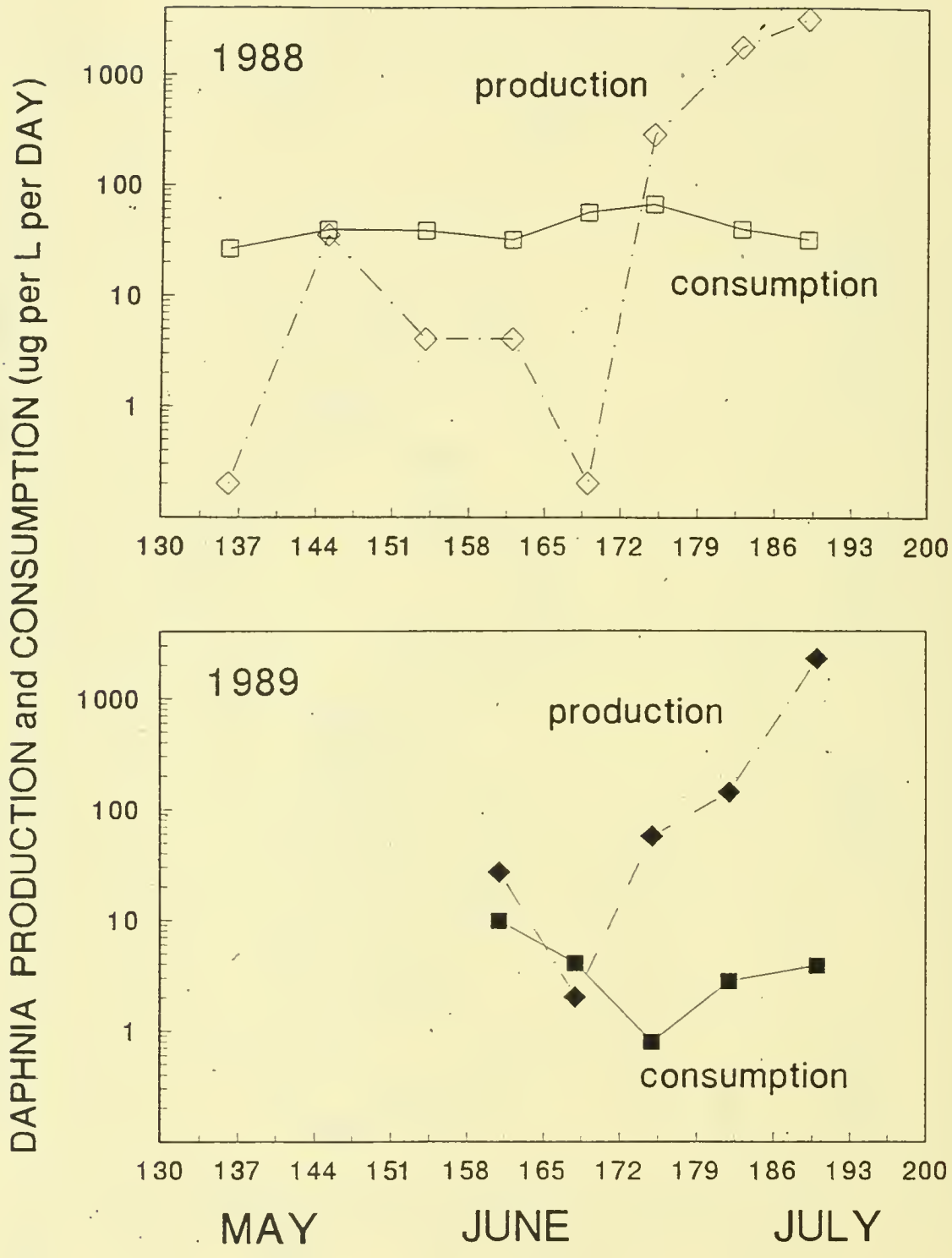
DAPHNIA PRODUCTION and CONSUMPTION (ug per L per DAY)
1988
production
consumption
1000
100
10
1
130 137 144 151 158 165 172 179 186 193 200
1989
production
consumption
1000
100
10
1
130 137 144 151 158 165 172 179 186 193 200
MAY
JUNE
JULY

FIGURE 7

SECCHI DEPTH (m)
4
3
2
1
0
10^0
10^1
10^2
10^3
10^4
DAPHNIA BIOMASS (ug per L)

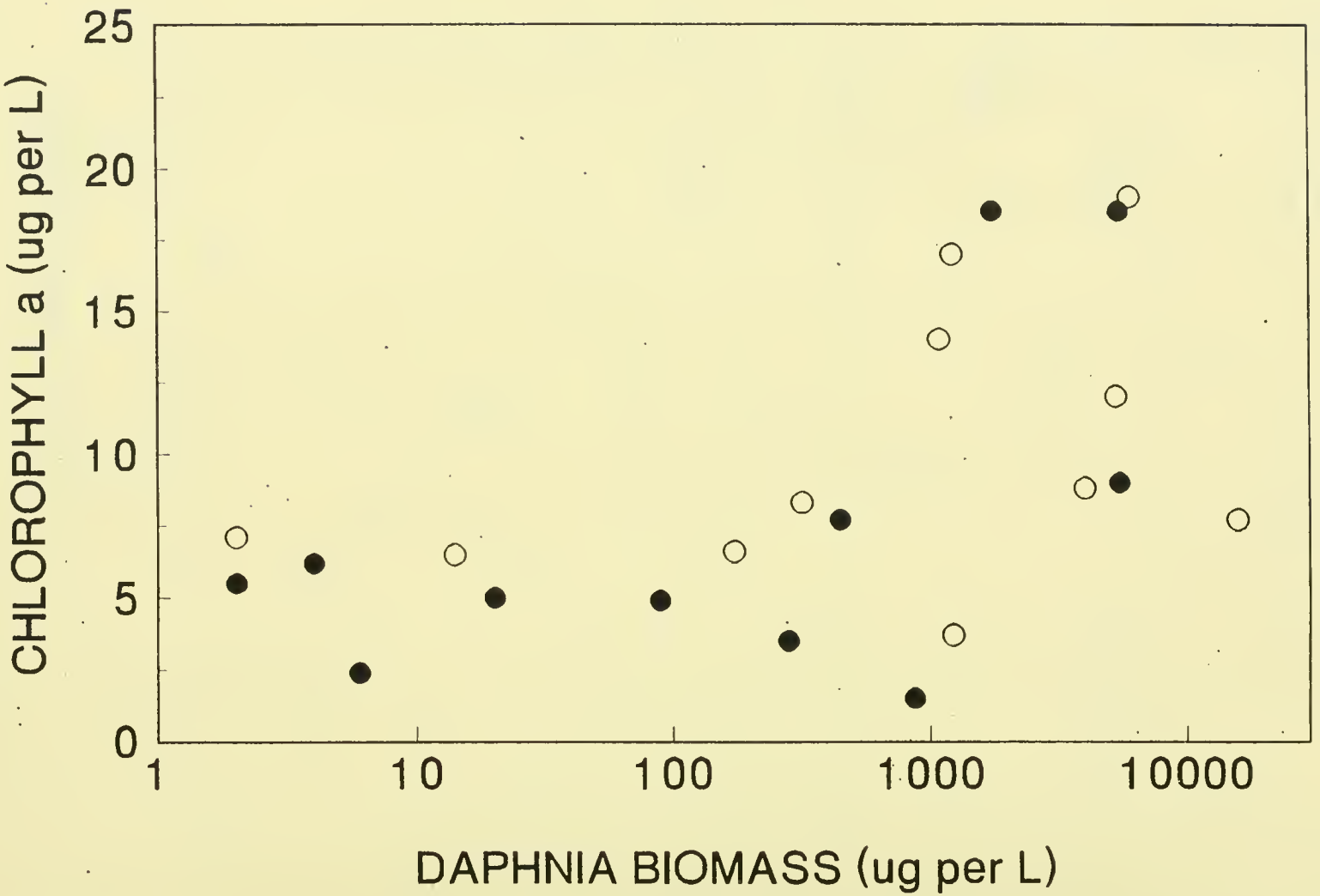
CHLOROPHYLL a (ug per L)
25
20
15
10
5
0
1
10
100
1000
10000
DAPHNIA BIOMASS (ug per L)

FIGURE 8

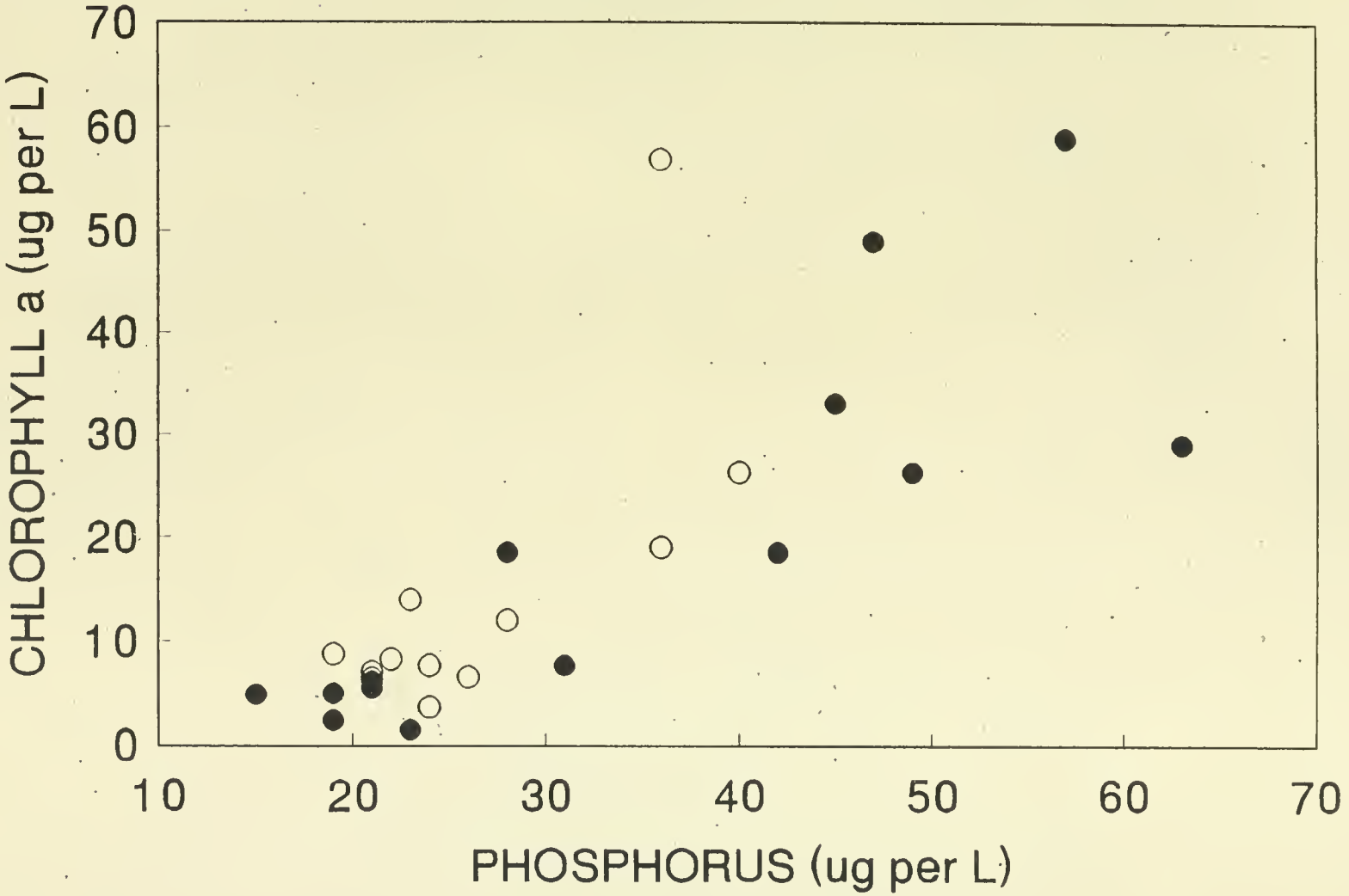
CHLOROPHYLL a (ug per L)
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
PHOSPHORUS (ug per L)

FIGURE 9